# Statistical assessment on determining local presence of rare bat species

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**Abstract** Surveying cryptic, sparsely distributed taxa using autonomous recording units, although cost-effective, provides imperfect knowledge about species presence. Summertime bat acoustic surveys in North America exemplify the challenges with characterizing sources of uncertainty: observation error, inability to census populations, and natural stochastic variation. Statistical uncertainty, if not considered thoroughly, hampers determining rare species presence accurately and/or estimating rangewide status and trends with suitable precision. Bat acoustic data are processed using an automated workflow in which proprietary or open-source algorithms assign a species label to each recorded highfrequency echolocation sequence. A false-negative occurs, if a species is actually present but not recorded and/or all recordings from the species are of such poor quality that a correct species identity cannot be assigned to any observation. False positives for a focal species are a direct result of the presence and incorrect identification of a recording from another species. We compare four analytical approaches in terms of parameter estimation and their resulting (in)correct decisions regarding species presence or absence using realistic data-generating scenarios for bat acoustic data within a simulation study. The current standard for deciding species presence or absence uses a multinomial likelihood ratio test p-value (MLE-metric) that accounts for known species misidentifications, but not imperfect detection and only returns a binary outcome (evidence of presence or not). We found that the MLE-metric had estimated median correct decisions less than 60% for presence and greater than 85% for absence. Alternatively, a multi-species count detection model was equivalent to or better than the MLE-metric for correct claims of rare species presence or absence using the posterior probability a species was present at a site and, importantly, provided unbiased estimates of relative activity and probability of occurrence, creating opportunities for reducing posterior uncertainty through inclusion of meaningful covariates. Single-species occupancy models with and without false-positive detections removed were insufficient for determining local presence because of substantially biased occurrence and detection probabilities. We propose solutions to potential barriers for integrating local, short-term and rangewide, long-term acoustic surveys within a cohesive statistical framework that facilitates determining local species presence with uncertainty concurrent with estimating species-environment relationships.

**Keywords**: Acoustic Survey, Autonomous Recording Units, Bayesian Hierarchical Model, Count Detection Model, False Positives, Imperfect Detection, North American Bat Monitoring Program, Occupancy Modeling, Sampling Design

# 1. INTRODUCTION

Decision-making in the face of uncertainty is a fundamental challenge for natural resource managers (Polasky et al., 2011). Recommendations related to a species conservation status under the U.S. Endangered Species Act (ESA 1973, as amended) are typically assessed at a rangewide extent using long-term monitoring datasets, when possible (e.g., Smith et al. 2018). Status assessments consider a species' persistence on the landscape under plausible scenarios for future conditions related to their known stressors (e.g., in the case of bats, impacts of climate change, energy development, forest management, and disease; Frick et al., 2020; Hoyt et al., 2021). Ideally, spatially extensive and longitudinal datasets are collated to fuel statistical models for estimating with uncertainty whether populations are increasing, decreasing, or stable over time under hypothetical scenarios (Erickson et al., 2014; Cheng et al., 2021). Once a species is deemed "threatened or endangered" under ESA, approval for a habitat alteration often requires a determination of species presence or absence within a potentially affected area to minimize possible "take" of vulnerable species (USFWS, 2020). Data collection to inform the permitting process, typically, relies on surveys over a shorter time period within a given project area (e.g., for Myotis sodalis and M. septentrionalis see USFWS, 2020). Our work is motivated by considering whether a common statistical 17 inference framework is available for addressing both rangewide status assessments and local 18 decisions regarding rare bat species presence using data collected by autonomous recording 19 units (ARUs)—acoustic surveys.

The observational unit for bat acoustic surveys is a high-frequency recording that can be

visualized using a spectrogram (Aodha et al., 2018). Many species can be recorded during a nightly interval at a specific deployment location (a "visit"). A nuance of bat acoustic data is that the sheer volume of echolocation sequences recorded during a visit necessitates an automated workflow for managing the recordings (Aodha et al., 2018). Recordings are processed using proprietary classification software or open-source machine learning algorithms to assign or label an echolocation sequence to a particular species (Acevedo et al., 2009; Sugai et al., 2018). Consequently, cross-species misidentifications—the wrong species is assigned to a recording—can be introduced during the automated classification process. Misclassifications at the recording level, if not accounted for, can propagate into visit-level false-positive and false-negative detections that can bias resulting statistical inferences (Clement et al., 2014; Chambert, Waddle, Miller, Walls and Nichols, 2018; Banner et al., 2018).

To minimize the potential for a software program to "confuse" echolocation sequences among bats in the genus *Myotis* and *Lasiurus borealis*, the "maximum likelihood" metric was developed based on misclassification rates calculated from high-frequency recordings with known species identities (the "MLE"-metric; Britzke et al., 2002). The MLE-metric is the current standard supported by the U.S. Fish and Wildlife Service (USFWS) for determining local presence for two rare bat species, *M. septentrionalis* and *M. sodalis*. To ensure consistency in application among project areas, the USFWS independently approves automated bat acoustic identification software programs (i.e., auto-classifier) for acoustic survey work (USFWS, 2020). The MLE-metric returned by approved software is then used to make a decision about species presence at a site. For regulatory purposes, the USFWS considers *M. septentrionalis* and *M. sodalis* present at a local site, if one or more survey nights (visits) returns an MLE-metric less than 0.05. To date, no work has explored the performance

of the MLE-metric for determining local bat presence using a statistical simulation study.

The benefit of our simulation investigation is that the true state (species present or not)

known and available for investigating how often the MLE-metric approach arrives at a

correct decision under different data-generating scenarios for bat acoustic data.

We consider whether Bayesian occupancy models are a viable alternative to the MLE-49 metric for determining local presence of rare bat species within the same simulation study. Often biologists summarize the nightly recordings to detection/non-detection (one or zero) 51 for a single focal species and apply occupancy models for statistical analyses (Rodhouse et al., 2012). Standard occupancy models account for imperfect detection (MacKenzie et al., 2002) at the visit level, which for bat ARU data, arise because a species is actually present but not recorded, and/or all recordings from the species are of such poor quality that a correct species identity cannot be assigned to any observation (Banner et al., 2018). A visitlevel false-positive detection is the consequence of the auto-classifier incorrectly assigning the focal species label to at least one recording. To proceed with standard occupancy modeling, one option is to effectively override or remove false-positive detections prior to statistical analyses (Barré et al., 2019). Currently, for North American bats, false-positive detections are removed either by using the "MLE-metric" from the computer software at a nightly level (visit-level) (e.g., Nocera et al., 2019b; Rojas et al., 2018), or by way of human vetters that are considered "experts" (Rojas et al., 2018; Banner et al., 2018). The human vetters follow a regional "key" or established rule-set to confirm at least 1-5 recordings are assigned the correct species label (e.g., Reichert et al., 2018). Occupancy modeling provides explanatory inferences about species probability of occurrence and how those may relate to environmental gradients, such as elevation, percent forest, and terrain ruggedness (e.g., Wright et al., 2021). However, summarizing ARU data to a binary response may lack the resolution required for detecting more subtle population impacts from disease or disturbances (e.g., fire), creating temporally non-analog conditions that are spatially heterogeneous across a landscape (e.g., Law et al., 2018; Nocera et al., 2019a; Hyzy et al., 2020).

Recently, a Bayesian hierarchical model was developed for ARU data that provides estimates of species-specific activity at a local deployment location and estimates of site-level species occurrence associations with uncertainty (Wright et al., 2020; Stratton et al., in press 2022). The multi-species count detection model by Wright et al. (2020) utilizes the count of detections per species and avoids reducing the data to simply detection/non-detection for a nightly recording interval. The multi-species count detection model provides a potential bridge between two important objectives—broad-scale status and trends and local-scale decision making. In fact, we show the mathematical connection of the MLE-metric calculation (Britzke et al., 2002) and a posterior probability from the multi-species count detection model that allows for a direct comparison of these two methods for local-scale decision making (full details in Appendix S1). The key distinction between these approaches is that the count detection model allows for imperfect detection and inclusion of habitat and environmental conditions that inform and have the potential to improve determination of local presence for rare species.

We conduct a simulation-based assessment to compare the current USFWS regulatory
standard of using the MLE-metric for determining species presence at a site to the multispecies count detection model and two alternative implementations of single-species occupancy models. We focus on the relative performance of the analytical approaches in terms
of making a correct decision regarding species presence or absence at a specific location. A

concern when relying on statistical estimation for making a decision is whether the fitted
models recover the data-generating values with reasonable accuracy and precision; if not, the
ability to make a correct decision may be affected. Therefore, we include an investigation
into parameter estimation for the Bayesian modeling approaches to verify whether they are
statistically sound alternatives for application in local decision-making. Our work is motivated by our belief there is an unrealized opportunity in North American bat conservation to
inform both site-level decisions about rare species presence and estimate species occurrence
and relative activity related to environmental conditions using a unified statistical design
and modeling framework.

# 2. METHODS

In Section 2.1, we outline the two primary sampling designs used in North America for 101 collecting summertime bat acoustic data. The guidance differs because the intended spatial 102 scope of inference varied: a specific project area versus rangewide extents (Fig. 1 denoted 103 as Goal of Analysis). In Section 2.2, we provide details on the current USFWS standard for 104 determining local species presence based on the MLE-metric (denoted as grey pathway in 105 Fig. 1). Then in Section 2.3, we outline three Bayesian model-based approaches for bat ARU 106 data that we include because of their potential for estimating the probability a species occurs 107 locally and throughout its range (denoted as black pathways in Fig. 1). All the model-based options account for imperfect detection, but they differ in how species misclassifications are accounted for when estimating probability of occurrence (see Fig. 1). Finally in Section 2.4, we describe our simulation study design for comparing the four analytical approaches in terms of their ability to assign the correct state of species (present or absent) at a site. The
various factors we investigate were chosen because of their potential to influence estimating
model parameters or assigning the (in)correct state of species presence or absence at a site
(Fig. 1 denoted by dashed ovals with call-out boxes).

### 116 2.1 Summer Acoustic Bat Survey Guidelines

In North America, State and Federal regulations and policies require surveys to determine 117 local presence of at least five bat species or sub-species (Corynorhinus townsendii ingens, C. 118 t. virginianus, Myotis griscescens, M. septentrionalis, and M. sodalis) during the summer 119 maternity season when most vulnerable to disturbance from management actions, e.g., forest 120 harvesting, prescribed burning, surface mining, road construction and development (Silvis 121 et al., 2016). Summer survey guidelines for determining sensitive species probable presence 122 or absence to inform localized decisions are available from the U.S. Fish and Wildlife Service 123 (USFWS, 2020). Currently, USFWS guidelines are geared towards two particular at-risk 124 species that hibernate during the winter and day-roost in forests in the summer, M. septen-125 trionalis and M. sodalis. Data are collected using stationary ARUs, but the spatial unit of a site is approximately 0.5 km<sup>2</sup> in area or along a 1 km linear unit. Deployment periods 127 vary by target species and location, but generally are 8-9 precipitation-free nights for an areal project and 2 nights per km for linear. Typically, these data are then analyzed using the MLE-metric at the visit-level to make a decision regarding local species presence (Fig 1, grey pathway) before obtaining project clearance. We describe the MLE-metric calculation in Section 2.2. 132

Alternatively, an omnibus North American Bat Monitoring Program (NABat) designed 133 to provide summertime status and trend estimation rangewide for multiple species simulta-134 neously uses a common probabilistic master sample survey design for site selection (Larsen 135 et al., 2008). The master sample is based on a grid-based sample frame with 10-km x 10-136 km cells. Within each selected NABat grid-cell, between 2 to 4 locations are selected for 137 deploying ARUs for one to four nights (Loeb et al., 2015). The number of nights and lo-138 cations within a grid cell can be informed by estimated species detection probabilities and 139 field logistics (e.g., Rodriguez et al., 2019). NABat data have been analyzed at state-level 140 (Neece et al., 2019), regional (Rodhouse et al., 2019), and rangewide (Udell et al., 2022) 141 extents using various Bayesian hierarchical models. The inferential goals are typically to 142 predict occurrence probabilities at all surveyed and non-surveyed sites and also estimate 143 species-environment relationships with uncertainty. We consider a subset of the available 144 options for modeling bat acoustic data (described in Section 2.3) for our simulation inves-145 tigation because they also afford a pathway to site-level decisions about presence (Fig. 1, 146 black pathways).

#### $^{_{148}}$ 2.2 "MLE"-metric calculation

Britzke et al. (2002) introduced a MLE-metric for determining site-level species probable
presence based on the number of recordings labeled to a focal species by the auto-classifier
(hereafter, "autoID") during a given recording interval (e.g., one night or aggregated over
many nightly surveys). The approach explicitly acknowledges that autoIDs are subject to
false positives, and a false positive for one species is a direct result of the presence and

incorrect identification of a recorded echolocation sequence from another species. Britzke et al. (2002) constructed a likelihood ratio (LR) test for the null hypothesis of species absence as an approach to decide species presence after accounting for software inaccuracies.

Following Britzke et al. (2002),

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 $\phi_{k'k}$  = probability that a recording from species k is identified to species k'. For a community of K species, a matrix with dimensions  $K \times K$  is defined, where each row represents the software autoID result and each column is the true species identity,

 $\theta_k^B$  = relative frequency of species k in sampled community, where we use the superscript B on the parameter to denote that it is from the Britzke et al. (2002) method,

N = total number of high-frequency sequences recorded and identified, and

 $n_k$  = the number of recordings identified to species k (autoIDs).

The classification probabilities  $(\phi_{k'k})$  are assumed known and are based on a large set of voucher search-phase calls. From Britzke et al. (2002) "voucher calls were recorded from free flying bats in open areas with chemical light sticks on their backs such that the species emitting the echolocation call was known." The relative frequency of a species in the sampled community  $(\theta_k^B)$  are unknown parameters. The MLE-metric assumes a multinomial data likelihood for the total number of identifiable recordings and the number of autoIDs per species  $(n_1, \dots, n_K)$  with probabilities  $\sum_{k=1}^K \phi_{k'k} \theta_k^B$ ;

$$L(\mathbf{n}, \theta) \propto \prod_{i} \left( \sum_{k=1}^{K} \phi_{k'k} \theta_k^B \right)^{n_k}.$$
 (1)

The MLE-metric is the p-value from the likelihood ratio test with null hypothesis that

species k is absent from a site,  $\theta_k^B = 0$  in Eqn. 1, versus the alternative hypothesis that the species is present,  $\theta_k^B > 0$  in Eqn. 1. A p-value provides evidence against the null hypothesis — the probability of observing a test statistic at least as extreme (or more extreme) as what was observed, assuming the null hypothesis (species absence) and assumptions listed in Appendix S1 are reasonable.

Although the USFWS M. sodalis protocol determines species probable presence or ab-178 sence as the MLE-metric applied at a visit-level (USFWS, 2020), we aggregated counts of 179 autoIDs over all nightly recording sessions at a deployment location to both increase the 180 number of recordings (sample size) and for an equivalent comparison to the model-based 181 site-level decisions (denoted, "MLESite"; Appendix S1 and see Sec. 2.4.2). Current USFWS 182 guidance suggests using a conservative 0.05 as the cut-off in the decision-rule for determin-183 ing localized presence (if MLE-metric p-value < 0.05, claim species present; USFWS, 2020). 184 Hereafter, we denote the *MLESite* threshold value as  $\alpha$  because it represents the significance 185 level chosen for the hypothesis test (see Fig. 1). 186

# 2.3 Bayesian Models for Bat Acoustic Data

We explored three Bayesian modeling options for bat acoustic surveys (denoted by rounded rectangles in Fig. 1): 1) a standard single-species occupancy model that accounts for imperfect detection (denoted, "Naive"), 2) a single-species occupancy model with false-positive detections removed prior to analysis (denoted, "Remove"), and 3) a multi-species count detection model. The Naive and Remove approaches estimate probability of presence and detection for each species separately. Following notation from MacKenzie et al. (2002),

let  $i = \{1, ..., n\}$  index sites,  $j = \{1, ..., J\}$  visits. Then, the partially observed state of a site,  $Z_i$  is modeled as a Bernoulli random variable with probability  $\psi_i$  ( $Z_i = 1$  if the focal species occurs at site i; 0 otherwise). Presence (the Z-state) is imperfectly observed. The probability the focal species is detected at a site in which it occurs is denoted by p. Thus,  $Y_{ij}|_{Z_i} = 1 \sim Bernoulli(p_{ij} * z_i)$ , where  $y_{ij}$  is 1 if the focal species is detected at site i during visit j and 0 otherwise. Because  $y_{ij} = 1 \implies z_i = 1$ , the single-species occupancy model assumes no false-positive detections are made at the visit-level. Both the detection-level and occupancy-level of the model can be extended to include covariates that explain heterogeneity in p and  $\psi$  among visits or among sites (MacKenzie et al., 2002).

The difference between the Remove and Naive approaches lies in the construction of 203 the detection history matrices (MacKenzie et al., 2002). The detection history matrix is 204 defined as the  $n \times J$  matrix of the observed  $y_{ij}$  values for all (i, j). The Remove approach 205 pre-processes the autoID counts for each species prior to fitting a single-species occupancy 206 model. The pre-process step is achieved by implementing the MLE-metric with  $\alpha = 0.05$ 207 based on the total number of identified recordings per species during a visit in an attempt to 208 "Remove" false-positive errors prior to building the detection history matrix. The detection 209 history matrix had a '1' entered for a visit, if the MLE-metric is < 0.05, otherwise a '0' was 210 entered. Alternatively, the Naive approach assumes that if at least one autoID is assigned to 211 the focal species during a visit, then that species was present during the visit (i.e., a '1' entry, 212 otherwise a '0' entry). The *Naive* approach incorrectly assumes the software auto-classifier always assigns the correct species label to a recording. 214

The multi-species count detection model, a Bayesian hierarchical model, was developed for ARU data to account for the same properties noted by Britzke et al. (2002) that the

rate of false positives for a species was related to both the autoclassification error rates and
the presence and relative activity of other co-occurring bat species. In our application of
the multi-species count detection model, we assume a two-species case (denoted, "2sppCt").

We assume the same information required for the MLE-metric is available for use in the
2SppCt model. Specifically, we assume that the accuracy rates from the classifiers are known
and correct. Appendix S1 provides the mathematical connection between the MLESite
approach and the posterior probability from the 2SppCt, which allows for a comparison of
their (in)correct decisions about local presence within a simulation environment.

We briefly describe the multi-species count detection model, but see Wright et al. (2020) and Stratton et al. (in press 2022) for additional guidance on data requirements and Bayesian prior specification when the classification probabilities are assumed unknown and estimated jointly. Following notation from Wright et al. (2020), let  $i = \{1, ..., n\}$  index sites,  $j = \{1, ..., J\}$  visits to each site within a season, and  $k = \{1, ..., K\}$  index possible species available for recording during a study. For site i, species k was present (1) or not (0) with probability  $\psi_{ik}$  and we model this latent presence state as

$$Z_{ik} \sim \text{Bernoulli}(\psi_{ik}),$$
 (2)

then an appropriate link function (e.g., logit, probit) can be used to model site-level information to inform the probability a species occurred at a site  $(Z_i = 1)$  such as elevation or percentage forest cover. Given species k occurs at site i, the true number of echolocation

235 sequences (recordings) for a species is modeled as,

$$[Y_{ijk} \mid Z_{ik} = 1] \sim \text{Poisson}(\lambda_{ijk}),$$
 (3)

where  $\lambda_{ijk}$  is the expected (mean) number of recordings per night and  $\log(\lambda_{ijk})$  can be used to include covariates associated with relative bat activity during a site-night visit, such as nightly minimum temperature or average wind speed. In the count detection model, the probability of a false negative (zero recorded and/or identifiable calls even though species present at site) is estimable as,  $Pr(Y_{ijk} = 0|Z_{ik} = 1) = exp(-\lambda_{ijk})$ . The observed response data are the sum of autoIDs for each species  $(n_k)$  and are modeled as Poisson counts,  $[n_k|\mathbf{Z},\boldsymbol{\lambda},\boldsymbol{\phi}] = Poisson(\sum_{k'=1}^K Z_{ik'}\lambda_{ijk'}\phi_{kk'})$ .

### 2.4 Simulation Study Methods

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For our study, we assumed only two species because our exploration utilized computer 244 simulations and increasing to more species increased the computational demand. Our previ-245 ous work verified that the multi-species count detection model returns unbiased parameter 246 estimates when extended to bat assemblages composed of ten species (Stratton et al., in press 247 2022). Similarly, other work has established the overestimation of occupancy probabilities 248 when the *Naive* model is applied to datasets contaminated by false-positive detections from 249 an omnibus source (Royle and Link, 2006), but we include it for completeness. The Remove 250 approach has not been evaluated previously using a statistical simulation study, only with 251 empirical observations of M. septentrionalis (Rojas et al., 2018).

Our first objective was to compare the three model-based approaches for estimating both

the probability a species is detected (p) and the probability a species occurs  $(\psi)$ . Our second objective was to compare the MLESite and suitable model-based approaches in terms of their application for discerning site-level species presence or absence correctly within the same simulation framework. Because we know that automatic classifiers for bat acoustic data are not 100% accurate, we generated datasets of autoIDs contaminated by recording or 258 observation-level identification errors for two species (data were consistent with the 2SppCt 259 model). The chosen parameter settings reflected our current understanding of two species 260 (M. lucifugus and M. sodalis) that produce similar search-phase echolocation calls and tend 261 to co-occur, and display considerable overlap in habitat association for many areas (Ford 262 et al., 2005, Table 1). One species was assumed rare (e.g., M. sodalis) within a study area 263  $(\psi_1 = 0.25)$  and locally less active (relative activity rates averaging around 1 identifiable 264 recording per night). The second species was assumed more widespread (e.g., M. lucifuqus; 265  $\psi_2 = 0.75$ ) and more active (relative activity rates with on average 10 identifiable recordings 266 per night). 267

We considered five different simulation scenarios. Three scenarios reflected different (miss)-classification probabilities with varying contributions of false positive recordings from the common species ( $\phi$ , S1, S2, S3: Table 1). Scenario 1 assumed that the auto-classifier was 90% accurate for rare species recordings and only 65% accurate for a common species; consequently, the contribution of false positives from the common species were considerable at 35%. Scenario 2 assumed that the auto-classifier was only 65% accurate for rare species recordings, but the false positive contributions from a common species were lower with only 10% of recordings of the common species misidentified. Scenario 3 assumed the auto-classifier accuracy rate for both the rare and common species was low, respectively 65% and 60%. The

remaining two scenarios (S4 and S5) provided direct comparisons to Scenario 1, the classifier accuracy rates were assumed the same ( $\phi$  equal for S1, S4, and S5 in Table 1). Scenario 4 assumed a higher occurrence probability for the rare species ( $\psi_1 = 0.50$ , Table 1). Scenario 5 assumed higher relative activity of the rare species, thereby increasing the expected number of recordings classified during a nightly interval.

All scenarios were assumed to have 55 sites with 8 or 16 recording nights per site for 282 consistency with current guidelines from NABat and USFWS for the endangered M. sodalis 283 and the M. lucifugus, a candidate for possible listing. We simulated 50 datasets under each 284 scenario for both 8 and 16 visits, and applied all four analytical approaches to each dataset. 285 Again, for the MLE-metric calculations and the 2SppCt, we assumed that the auto-classifier 286 (in)accuracy rates were known without error. The three model-based approaches were fit 287 using NIMBLE (de Valpine et al., 2017, 2021). The different scenarios required different 288 iterations, warm-up, and thinning of the MCMC to exhibit good mixing of the chains and 289 evidence of convergence. Chains were visually assessed using traceplots, summarized with 290 the Gelman-Rubin diagnostic (Rhat) and the number of effectively independent samples 291  $(n_{eff})$  (Rhat,  $n_{eff}$  computed using rstan, Stan Development Team, 2020). Details for each 292 scenario are provided in Appendix S2. We assumed diffuse priors of  $[\psi_k] = Uniform(0,1)$ ; 293  $[p_k] = Uniform(0,1);$  and a weakly informative prior of  $[\lambda_k] = Gamma(\text{shape} = 2, \text{rate} = 2)$ 0.25), which is right skewed with the majority of the mass between 0 and 20 and a mean 295 of 8 (median 6.7) and represents a reasonable range of relative activity for the species we consider.

#### 2.4.1 Parameter Estimation

We compared estimated probability for rare species presence  $(\psi_1)$  and common species 299 presence  $(\psi_2)$  among the 2SppCt, Remove, and Naive approaches, as all three models pro-300 vided Bayesian posterior distributions for these parameters. For visualization, we reported the average of the 2.5\%, 50\%, and 97.5\% percentiles from the parameter posterior distributions over the 50 iterations of simulated data for all three models. We assessed estimation error (bias) and relative uncertainty conveyed by the 95% posterior intervals for all three models. Coverage was computed by calculating the proportion of simulated datasets that 305 resulted in 95% posterior intervals including the true data-generating values (Note: slight 306 deviations from nominal coverage are expected because of the small number (50) of simulated 307 datasets for each scenario). The Remove and Naive occupancy models provide an estimate 308 of detectability ( $p_1$  and  $p_2$  for both species), whereas the 2SppCt model provides an estimate 309 of species-specific relative activity ( $\lambda_1$  and  $\lambda_2$ ). 310

#### 2.4.2 Assessing site-level decisions regarding species presence (absence)

For each simulated dataset, we determined a site-level decision regarding a conclusion of species absent or present with all four approaches (MLESite, 2SppCt, Remove, Naive) for comparison to the true known state of species absent (Z=0) versus present (Z=1). We summarized the number of sites with a specific decision conditional on the known true state of species presence or absence for each dataset comprised of 55 sites.

The *MLESite* approach used the total number of autoIDs classified to each species aggregated over the nightly surveys (8 or 16 visits) to arrive at a site-level decision of species

presence or absence. The *MLESite* decision-rule is based on a threshold that is related to a maximum tolerance for making a Type I error (claiming species was present when actually absent). We explored different thresholds ( $\alpha$ ) for the decision-rule embedded in the *MLE-Site* approach for concluding species presence (MLE-metric  $< \alpha$ ) or absence (MLE-metric  $\geq \alpha$ ). We considered  $\alpha = 0.05, 0.1, 0.15$ , and 0.2, which represents a reasonable range of tolerances for making Type-I errors (erroneously concluding species presence). These results are presented in Appendix S2.

The model-based approaches (2SppCt, Remove, Naive) arrived at a site-level decision 326 by using the Bayesian posterior probability a species occurs at a site. The model-based 327 approaches used the posterior mean of the Z-state for each site  $(Pr(Z_i = 1|y))$  compared 328 to a threshold  $(z_{cutoff})$  to make a site-level decision about species presence or absence. The 329 decision-rule was defined as,  $Pr(Z_{ik} = 1|y) > z_{cutoff} \implies$  species k was claimed present 330 at site i, otherwise species k was claimed absent at site i. We considered  $z_{cutoff}$  values of 331 0.05, 0.25, 0.5, 0.75, and 0.95 to represent a range of decision-rules. Smaller  $z_{cutoff}$  values 332 increased the number of sites with a decision of species present. Conversely, larger values of 333  $z_{cutoff}$  increased the number of sites with the state of species absent assigned. The threshold 334 investigation results are presented in Appendix S2. 335

# 3. Results

Generally, we found that changing the classifier accuracy from 0.90 to 0.65 and recordinglevel false-positive rate from 0.35 to 0.10 for the rare species did not impact 2SppCt parameter
estimation or the site-level decisions of MLESite and 2SppCt because we assumed those val-

ues were known and correct (results in Appendix S2). The scenario where both species had
poor auto-classifiers (true classification rates of 0.65 for rare species and 0.60 for common
species in Scenario 3, Table 1) led to poor estimation of the relative activity using 2SppCt
across the 50 simulated datasets (Appendix S2). The unstable results suggest a minimum
accuracy for species classification should be established, which was consistent with the rigorous testing required by the USFWS to approve software for rare species surveys (USFWS
and USGS, 2019).

We include all results for the common, easily detected species in Appendix S2. The results 347 showed little variability among scenarios and near perfect correct site-level decisions among 348 the 5 data-generating scenarios we investigated. This is not very surprising because site-level 349 decisions about species presence are robust when a species has very high probability of being 350 detected acoustically, when present. The contributions of recording-level false-positives from 351 the rare species were too infrequent relative to the number of correct identifications of the 352 common species to bias the decision outcome. The utility of including the "common" species, 353 statistically, is as the source of recording-level false-positives for the rare species. 354

In the following sections, we explore parameter estimation for the model-based approaches (Section 3.1) and then compare MLESite approach to suitable model-based approaches for determining whether the rare species was present at a site (Section 3.2). We assume the classifier was 90% accurate identifying the rare species with a substantial source of false positives contributed by the common species recordings (35%). We focus on comparing three scenarios to investigate whether increasing the occurrence probability for the rare species from  $\psi_1 = 0.25$  to  $\psi_1 = 0.5$  (denoted,  $[\psi = 0.25, \lambda = 0.3]$  versus  $[\psi = 0.5, \lambda = 0.3]$ ) or increasing the detection probability for the rare species from  $p_1 = 0.25$  to  $p_1 = 0.5$  (denoted,

 $[\psi=0.25,\lambda=0.3]$  versus  $[\psi=0.25,\lambda=0.7]$ ) influenced model parameter estimates or site-level decisions.

# Naive, Remove, and 2SppCt model estimation for rare speciesoccurrence and detection probabilities

The count detection model is the most realistic data-generating model for bat acoustic 367 data currently in the literature, and given that simulated datasets were generated under 368 this model, it was not surprising that the 2SppCt version consistently returned unbiased  $\psi$ 369 estimates for the rare species (Fig. 2 top row with additional results in Appendix S2: Figures 370 S1-S2). The posterior estimates for relative activity or the average number of recordings per 371 species were unbiased and 95% coverage was achieved for most scenarios, as expected (Fig. 372 2 bottom row and Appendix S2: Figure S1-S2). There was a slight reduction in uncertainty 373 (narrower posterior intervals) for the rare species with 16 rather than 8 visits (Appendix S2 Figures S1-S2).

The *Remove* approach overestimated probability of presence (Fig. 2 top row) and underestimated the probability of detection regardless of the assumed average occurrence or relative activity (Fig. 2 middle row). The small detection probabilities explains the larger uncertainty for occurrence probabilities using *Remove* (Fig. 2). The posterior intervals based on the *Remove* approach were more noticeably reduced by doubling the number of visits at a site from 8 to 16 (Appendix S2 Figures S1-S2).

The *Naive* approach consistently overestimated rare species occurrence probability (Fig. 2 top row) and probability of detection (Fig. 2 middle row) for all scenarios because of

false-positive detections contributed from a common species. These parameter estimates
translated to an "always present" decision for every site. The severe bias in parameter
estimation using the *Naive* occupancy model suggested its application for assessing rare bat
species presence requires caution and justification that no false-positives occur.

# $^{338}$ 3.2 *MLESite* versus *Remove* or $^{2}SppCt$ model performance for determining local species presence

We present our investigation into whether the threshold value specified in the decision-390 rule influenced the median proportion of sites assigned the correct state of rare species 391 present or absent in Appendix S2. We used cut-off values that balanced the correct versus 392 in-correct decision rates regarding species presence or absence at a site in the comparisons 393 we highlight (Fig. 3). The MLESite decision-rule for species presence was p-value < 0.10394 and p-value > 0.10 for species absence at a site. The posterior probabilities from 2SppCtand Remove were used with a threshold specific to the desired decision of species presence or absence: decision-rule of Pr(Z = 1|y) > 0.75 for species absence (protecting against erroneous determination of species presence) and a decision-rule of Pr(Z=1|y) > 0.25 for species presence (protecting against erroneous determination of species absence) at a site. 399 Regardless of the assumed occurrence and relative activity for the rare species in our sim-400 ulations, the 2SppCt model outperformed the MLESite approach for correctly determining 401 a species was present at a site (Fig. 3 top left panel). The 2SppCt model median correct 402 decision-rate for presence increased from 0.78 to 1 as the occurrence probability increased 403 from 0.25 to 0.50, and the variability in correct decision-rates decreased. The MLESite median correct decision-rate for presence was improved when the assumed average number of recordings increased from 5 to 11 over the entire survey duration (16 nights of recording).

However, the median proportion of correct decisions for presence was always less than 0.5 for the *MLESite* (Fig. 3. top left panel). The *Remove* approach always returned a decision of species presence, regardless of the data-generating values (Fig 3. top left panel).

Another way to explore the performance for informing local decisions is to consider the 410 median proportion of sites with incorrect decisions of species absent when truly present (Fig. 411 3 bottom left panel, notice bottom panel is essentially a mirror image of the corresponding 412 top panel). The 2SppCt model consistently had the lowest median incorrect decision-rates 413 compared to MLESite and Remove approach regardless of the assumed relative activity or 414 occurrence probabilities (Fig. 3 bottom left panel). Again, the performance for the 2SppCt 415 model improved when the assumed occurrence probability for a rare species was 0.50 and the 416 MLESite incorrect decision-rate was reduced by increasing the expected number of nightly 417 recordings. The *Remove* approach infrequently resulted in a decision of species absence (very 418 few points graphed in bottom left panel Fig. 3). 419

For all the approaches we explored, the correct decision-rates for species absence were less variable with no clear differences related to assumed relative activity or occurrence probabilities (Fig. 3 right panels). The 2SppCt model was equivalent to or better than the MLESite approach for determining a rare species was absent at a site with both having median correct decisions > 90% of the time (Fig 3., bottom right panel). The Remove had the lowest correct decision-rates for species absence (Fig 3. lower right panel).

Both the 2SppCt and MLESite had consistently the lowest median incorrect decisionrate for claiming a rare species was present when truly absent (Fig. 3, top right panel). Note the *MLESite* had a median incorrect decision-rate of approximately 10%. As expected,
the number should be close to the cut-off value or α used to make a decision because the *MLESite* was based on a frequentist hypothesis test. The *Remove* approach had consistently
the highest median incorrect decision-rate (approx. 25%) regarding local absence because
most sites were assigned the incorrect state of rare species presence (Fig. 3, top right) due
to the bias in the occurrence and detection parameter estimates (Fig. 2, top two rows).

# 4. Discussion

Our simulation investigation indicated that the multi-species count detection model (in 435 the two species case) was equivalent to or better than the current USFWS standard for 436 determining local species presence, which opens up possibilities for integrating summertime 437 acoustic datasets within a common statistical inference framework. Below, we outline the 438 key findings for the four approaches (MLESite, 2SppCt, Remove and Naive) compared under 430 realistic data-generating scenarios for bat ARU data. Then based on our simulation findings, 440 we describe future field investigations that, in coordination with statistical method develop-441 ment, could provide huge dividends for bat conservation. We conclude with a discussion on statistical considerations prior to combining datasets from the different summertime acoustic surveys for rare bats and provide suggestions for sound data integration and Bayesian inferences with uncertainty in future. We found that applying the MLE-metric at a site-level (MLESite) had median correct decisions less than 60% for species presence with most scenarios ranging between 20% and 30%, but greater than 85% for species absence (ranging between 80% and 90%). The *MLE*-

Site had reasonable correct decision-rates for absence consistent with its intended purpose of null hypothesis testing for species absence (Section 2.2). However, to increase the correct decision-rate for species presence requires increasing the threshold-value ( $\alpha$ ) and/or increasing the total number of identified recordings (N) and the expected number of recordings identified to each species  $(E(n_k))$  in Eqn. 1; de Jong et al., 2019). Practically, a larger 453 sample size could result from aggregating recordings over more visits to a site, orienting 454 ultrasonic microphones to reduce interference that hampers recording quality (Loeb et al., 455 2015, chapter 4), and/or strategic placement of detectors in preferred habitats of the focal 456 species within the project area (e.g., for M. sodalis and M. septentrionalis upland and ri-457 parian forested conditions; Menzel et al., 2001; Silvis et al., 2016). However, data collected 458 using such a preferential sampling design are no longer representative of a larger collection of 459 sites (statistical population). Although the MLESite accounts for observation-level misclas-460 sifications, the information output is only a binary decision of species presence or absence 461 and potential sources of meaningful ecological variation and imperfect detection are ignored 462 (Fig. 1, denoted by grey pathway). 463

We propose an alternative to *MLESite* is to consider the multi-species count detection model. We found, in the two species case, that *2SppCt* had equivalent or greater correct claims of rare species presence (median > 75%) or absence (median > 80%) at a site. The count detection model was developed with the same underlying assumptions as *MLESite*, but can be modified and tuned for different applications. For example, variables that characterize differences in recording conditions (e.g., nightly temperature Gorman et al., 2021) or deployment locations (e.g., near water features, flyway, interior forest, etc; Ford et al., 2005) can be exploited to adjust inferences appropriately for nightly recording sessions that had no or very few bat calls detected. Depending on the spatio-temporal sampling design underlying an application, additional parameters can be included that model spatial correlation in
probability of occurrence (Eqn. 2) and/or temporal correlation in relative activity (Eqn. 3)
using Gaussian processes (Gelfand and Schliep, 2016; Wright et al., 2021). Importantly, the
count detection model allows for deeper insights into species-environment relationships in
both relative bat activity and presence. These estimated associations, when underpinned by
a probabilistic survey design, could be used to improve prediction of rare species occurrence
at a site thereby increasing the utility of bat ARU surveys to fulfill the goals of ecological
research and regulatory compliance information needs.

Our findings are consistent with previous work that urges caution in the application of the 481 Naive single-species occupancy model for ARU data subject to observation-level false pos-482 itives introduced during the automated classification process (Chambert, Campbell Grant, 483 Miller, Nichols, Mulder and Brand, 2018). The severe overestimation of occurrence and de-484 tection probabilities translated into essentially a conclusion of the rare species always being 485 present because the common species was always available to contribute false-positive detec-486 tions. We suggest the Naive approach should only be considered when the autoclassifier 487 is 100% accurate for all species that emit potentially overlapping echolocation sequences. 488 Even a small source of false-positive detections (< 5%) can bias occupancy model parameter estimates and, consequently, lead to an incorrect conclusion that a species is present within an area (Miller et al., 2013; Chambert et al., 2015)

However, applying the MLE-metric at the visit-level to "remove" false-positives prior to model fitting (i.e., the *Remove* approach) resulted in many sites where the species truly occurred with zero detections. Our findings that occurrence probabilities were overestimated

and detection probabilities severely underestimated were consistent with field-based comparisons of our *Remove* occupancy model to site confirmation false-positive models for M. septentrionalis (Rojas et al., 2018). As a simple demonstration of the ramifications parameter estimation bias can have on site-level decisions; a site with zero detections and the data-generating values we specified in Scenario 1 would have 0.003 posterior probability that 490 a species occurred (Table 1; MacKenzie et al., 2002). However, using the biased average posterior estimates based on the Remove model with 16 nights, the probability would be 501 0.40. An always present decision is perhaps satisfactory from a conservative conservation 502 stand-point to ensure the minimization of potential "take," but also may incorrectly attribute 503 habitat associations or correlates to a rare species that might divert or misallocate habitat 504 management and protection efforts. Based on our simulations, relying on the MLE-metric 505 at a visit-level as a means to remove false-positives detections was not sufficient for model-506 ing bat acoustic datasets; however, application in real-world conditions with potentially a 507 greater number of identified recordings and a larger bat species pool could present a different 508 perspective. 509

Our findings suggest the need for follow-up field studies that compare the *MLESite*, Remove approach, and the multi-species count detection model for determining species presence or absence using empirical data with a larger species assemblage. In our simulations, we assumed the true classifier accuracy rates were known and constant for all visits and sites. If these assumptions are not met the parameter estimates for  $\lambda$  and  $\psi$  would be biased and decisions based on the *MLESite* and count detection model potentially compromised. Curating local to regional calibration or confirmation datasets that tune the classification probabilities to real-world recording conditions could substantially improve rare species decisions and provide significant cost reductions for studies that employ human experts to verify
the assigned species to a recording (autoIDs; see Stratton et al., in press 2022). Ideally,
future work would consider co-locating ARU-based surveys with other field methods (known
roosts or mist-netting) that provide near definitive evidence that a rare species was actually
present (e.g., Miller et al., 2015; Rojas et al., 2018). Pairing such short-term field investigations with statistical method development increases the potential for both lines of inquiry
to improve conservation decision-making for rare bat populations.

Our simulations demonstrate that the multi-species count detection model holds promise 525 as a cohesive statistical inference framework for leveraging both local, targeted data collec-526 tion with rangewide probabilistic sampling to inform regional assessments and could reduce 527 uncertainty regarding local species presence. However, prior to integrating empirical datasets 528 that are collected under different objectives and survey protocols, the potential misalignment 529 in how sites are selected (spatial design), the grain size of a site (spatial resolution), and the 530 guidance on how field data are collected (response design) should be considered thoroughly. 531 For summertime bat acoustic surveys in North America, the main difference between the 532 NABat and USFWS protocols is the definition of a "site" (Sect. 2.1) because of the different 533 intended objectives. The omnibus NABat program defines a "site" as a  $10\text{-km} \times 10\text{-km}$ 534 grid cell based on average assumed dispersal distances (Loeb et al., 2015). For regulatory 535 project clearance prior to conducting activities within suitable summertime M. sodalis and 536 M. septentrionalis habitat, a site is defined as a 0.5-km<sup>2</sup> area (USFWS, 2020). The difference in analytical unit should not prevent integrating datasets gathered under the different sampling designs. In fact, a straightforward extension of the count detection model to a multi-scale parameterization that estimates an availability parameter and specifies an intermediate latent-level for rare species presence/absence at a specific detector location (e.g.,
Nichols et al., 2008) provides a reasonable statistical inference framework for a combined
dataset. The same model would allow for estimating grid-cell level species occurrence and
information from other survey sites and could be leveraged to improve the decisions made
at specific locations within a grid cell.

Minimal alterations to the summertime acoustic survey designs are needed to achieve 546 robust data integration of the regulatory survey data within the broader NABat framework. 547 The NABat guidance already suggested having both spatial and temporal replication within a grid cell (Loeb et al., 2015). Therefore, the only potential modification would be to increase 540 the number of nights to be consistent with USFWS guidance for **some** detector locations. 550 Also, local site selection for which habitats are optimal for detecting sensitive species need not 551 be changed, the information (metadata) characterizing the habitat surrounding the detector 552 location can be included in an integrated model as covariates for relative activity and local 553 availability, thereby adjusting for the preferential detector placement within a grid cell. For 554 example, the putative day-roosting and foraging habitat of M. septentrionalis and M. sodalis 555 in eastern North America is upland and riparian forested conditions (Gorman et al., 2022). 556 The NABat acoustic survey design suggests selecting different habitat features within a grid 557 cell to maximize the potential for detecting the full suite of species. The practical hurdle is properly measuring and archiving the local habitat in a consistent manner among survey 559 efforts. The NABat community of practice could provide the mechanism for developing consistent and compatible data fields about ARU summertime surveys and the online data submission portal facilitates the upload and download of both the design and response data for species assessments (Reichert et al., 2021).

In addition to the follow-up field investigations that we outlined and the clear potential for data integration of summertime acoustic survey data within the multi-species count detection modeling framework; we suggest an opportunity exists to exploit a full Bayesian statistical decision analysis (BDA) for rare species decision-making. A BDA combines the posterior probability that a species was present with a loss or risk function to determine the potential choice (claim species present or claim species absent) that has the lowest expected 569 risk (Williams and Hooten, 2016). A loss function could be developed with decision- and 570 policy-makers input regarding whether an erroneous claim of species absence or species 571 presence was more detrimental across a suite of stewardship actions and outcomes (Wade, 572 2000). For example, the economic cost of halting or modifying a forest management action 573 or an infrastructure project due to an incorrect decision of rare species absence versus the 574 potential loss of proceeding and increasing the possible accidental "take" for an endangered 575 species, if the species was truly present. The decision-rule for species presence would be 576 based on the decision outcome with the lowest expected risk. However, for some situations 577 there could be little distinction between the two outcomes expected risk values, but the full 578 uncertainty in the data and a clear articulation of the losses provide added transparency in 570 decision-making.

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# References

- 593 Acevedo, M. A., Corrada-Bravo, C. J., Corrada-Bravo, H., Villanueva-Rivera, L. J. and
- Aide, T. M. (2009), 'Automated classification of bird and amphibian calls using machine
- learning: A comparison of methods', Ecological Informatics 4(4), 206–214.
- Aodha, O. M., Gibb, R., Barlow, K. E., Browning, E., Firman, M., Freeman, R., Harder, B.,
- Kinsey, L., Mead, G. R., Newson, S. E., Pandourski, I., Parsons, S., Russ, J., Szodoray-
- Paradi, A., Szodoray-Paradi, F., Tilova, E., Girolami, M., Brostow, G. and Jones, K. E.
- (2018), 'Bat detective deep learning tools for bat acoustic signal detection', PLOS Com-
- putational Biology 14(3), 1–19.
- Banner, K. M., Irvine, K. M., Rodhouse, T. J., Wright, W. J., Rodriguez, R. M. and Litt,
- A. R. (2018), 'Improving geographically extensive acoustic survey designs for modeling
- species occurrence with imperfect detection and misidentification', Ecology and Evolution
- 8(12), 6144–6156.
- Barré, K., Le Viol, I., Julliard, R., Pauwels, J., Newson, S. E., Julien, J.-F., Claireau,
- F., Kerbiriou, C. and Bas, Y. (2019), 'Accounting for automated identification errors in
- acoustic surveys', Methods in Ecology and Evolution 10(8), 1171–1188.
- Britzke, E., Murray, K., Heywood, J. and Robbins, L. (2002), The Indiana bat: Biology and
- management of an endangered species, Austin, Texas: Bat Conservation International,
- chapter Acoustic Identification, pp. 221–225.
- 611 Chambert, T., Campbell Grant, E. H., Miller, D. A. W., Nichols, J. D., Mulder, K. P. and

- Brand, A. B. (2018), 'Two-species occupancy modeling accounting for species misidentifi-
- cation and nondetection', Methods in Ecology and Evolution 9(6), 1468–1477.
- Chambert, T., Miller, D. A. W. and Nichols, J. D. (2015), 'Modeling false-positive detections
   in species occurrence data under different study designs', *Ecology* 96(2), 332–339.
- 616 Chambert, T., Waddle, J. H., Miller, D. A. W., Walls, S. C. and Nichols, J. D. (2018), 'A
- new framework for analysing automated acoustic species detection data: Occupancy esti-
- mation and optimization of recordings post-processing', Methods in Ecology and Evolution
- **9**(3), 560–570.
- 620 Cheng, T. L., Reichard, J. D., Coleman, J. T. H., Weller, T. J., Thogmartin, W. E., Reichert,
- B. E., Bennett, A. B., Broders, H. G., Campbell, J., Etchison, K., Feller, D. J., Geboy, R.,
- Hemberger, T., Herzog, C., Hicks, A. C., Houghton, S., Humber, J., Kath, J. A., King,
- R. A., Loeb, S. C., Massé, A., Morris, K. M., Niederriter, H., Nordquist, G., Perry, R. W.,
- Reynolds, R. J., Sasse, D. B., Scafini, M. R., Stark, R. C., Stihler, C. W., Thomas, S. C.,
- Turner, G. G., Webb, S., Westrich, B. J. and Frick, W. F. (2021), 'The scope and severity
- of White-nose syndrome on hibernating bats in North America', Conservation Biology
- **35**(5), 1586–1597.
- <sup>628</sup> Clement, M. J., Rodhouse, T. J., Ormsbee, P. C., Szewczak, J. M. and Nichols, J. D. (2014),
- 'Accounting for false-positive acoustic detections of bats using occupancy models', Journal
- of Applied Ecology **51**(5), 1460–1467.
- de Jong, V. M. T., Eijkemans, M. J. C., van Calster, B., Timmerman, D., Moons, K. G. M.,
- Steverberg, W. and van Smeden, M. (2019), 'Sample size considerations and predictive

- performance of multinomial logistic prediction models', Statistics in Medicine **38**(9), 1601–1619.
- de Valpine, P., Paciorek, C., Turek, D., Michaud, N., Anderson-Bergman, C., Obermeyer, F.,
- Wehrhahn Cortes, C., Rodrìguez, A., Temple Lang, D. and Paganin, S. (2021), 'NIMBLE:
- MCMC, particle filtering, and programmable hierarchical modeling'. R package version
- 638 0.11.0.
- de Valpine, P., Turek, D., Paciorek, C., Anderson-Bergman, C., Temple Lang, D. and Bodik,
- R. (2017), 'Programming with models: writing statistical algorithms for general model
- structures with NIMBLE', Journal of Computational and Graphical Statistics 26, 403–
- 642 413.
- Erickson, R., Thogmartin, W. and Szymanski, J. (2014), 'BatTool: an R package with gui
- for assessing the effect of White-nose syndrome and other take events on Myotis spp. of
- bats', Source code for biology and medicine 9.
- 646 Ford, W. M., Menzel, M., Rodrigue, J., Menzel, J. and Johnson, J. (2005), 'Relating bat
- species presence to simple habitat measures in a central Appalachian forest', Biological
- Conservation 126(4), 528-539.
- <sup>649</sup> Frick, W. F., Kingston, T. and Flanders, J. (2020), 'A review of the major threats and
- challenges to global bat conservation', Annals of the New York Academy of Sciences
- **1469**(1), 5–25.
- 652 Gelfand, A. and Schliep, E. (2016), 'Spatial statistics and gaussian processes: A beautiful
- marriage', Spatial Statistics 18(A), 86–104.

- Gorman, K., Deeley, S., Barr, E., Freeze, S., Kalen, N., Muthersbaugh, M. and Ford, W.
- 655 (2022), 'Broad-scale geographic and temporal assessment of northern long-eared bat (My-
- otis septentrionalis) maternity colony landscape association', Endangered Species Research
- **47**, 119–130.
- 658 Gorman, K. M., Barr, E., Ries, L., Nocera, T. and Ford, W. (2021), 'Bat activity pat-
- terns relative to temporal and weather effects in a temperate coastal environment', Global
- 660 Ecology and Conservation **30**, 1–13.
- 661 Hoyt, J. R., Kilpatrick, A. M. and Langwig, K. E. (2021), 'Ecology and impacts of White-
- nose syndrome on bats', Nature Review Microbiology 19, 196–210.
- 663 Hyzy, B. A., Russell, R. E., Silvis, A., Ford, W. M., Riddle, J. and Russell, K. (2020),
- 'Occupancy and detectability of northern long-eared bats in the lake states region', Wildlife
- Society Bulletin 44(4), 732–740.
- 666 Larsen, D. P., Olsen, A. R. and Stevens, D. L. (2008), 'Using a master sample to inte-
- grate stream monitoring programs', Journal of Agricultural, Biological, and Environmental
- Statistics **13**(3), 243–254.
- Law, B. S., Doty, A., Chidel, M. and Brassil, T. (2018), 'Bat activity before and after a severe
- wildfire in Pilliga forests: Resilience influenced by fire extent and landscape mobility?',
- Austral Ecology 43(6), 706–718.
- Loeb, S. C., Rodhouse, T. J., Ellison, L. E., Lausen, C. L., Reichard, J. D., Irvine, K. M.,
- Ingersoll, T. E., Coleman, J. T., Thogmartin, W. E., Sauer, J. R., Francis, C. M., Bayless,
- M. L., Stanley, T. R. and Johnson, D. H. (2015), A plan for the North American Bat

- Monitoring Program (NABat), General Technical Report SRS-208, U.S. Department of
- Agriculture, Forest Service, Southern Research Station, Asheville, NC.
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A. and Langtimm,
- 678 C. A. (2002), 'Estimating site occupancy rates when detection probabilities are less than
- one', Ecology 83(8), 2248-2255.
- 680 Menzel, M., Menzel, J., Carter, T., Ford, W. and Edwards, J. (2001), Review of the forest
- habitat relationships of the Indiana bat (Myotis sodalis), General Technical Report NE-
- 284, USDA Forest Service, Newtown Square, PA.
- 683 Miller, D. A. W., Bailey, L. L., Campbell Grant, E. H., McClintock, B. T., Weir, L. A. and
- Simons, T. R. (2015), 'Performance of species occurrence estimators when basic assump-
- tions are not met: a test using field data where true occupancy status is known', Methods
- in Ecology and Evolution 6(5), 557-565.
- 687 Miller, D. A. W., Nichols, J. D., Gude, J. A., Rich, L. N., Podruzny, K. M., Hines, J. E.
- and Mitchell, M. S. (2013), 'Determining occurrence dynamics when false positives occur:
- Estimating the range dynamics of wolves from public survey data', *PLOS ONE* 8(6), 1–10.
- Neece, B. D., Loeb, S. C. and Jachowski, D. S. (2019), 'Implementing and assessing the
- efficacy of the north american bat monitoring program', Journal of Fish and Wildlife
- Management 10(2), 391-409.
- Nichols, J. D., Bailey, L. L., JR., A. F. O., Talancy, N. W., Grant, E. H. C., Gilbert,
- A. T., Annand, E. M., Husband, T. P. and Hines, J. E. (2008), 'Multi-scale occupancy

- estimation and modelling using multiple detection methods', Journal of Applied Ecology

  45(5), 1321–1329.
- Nocera, T., Ford, W. M., Silvis, A. and Dobony, C. A. (2019a), 'Patterns of acoustical activity of bats prior to and 10 years after WNS on Fort Drum Army Installation, New
- York', Global Ecology and Conservation 18, e00633.
- Nocera, T., Ford, W., Silvis, A. and Dobony, C. (2019b), 'Let's agree to disagree: Comparing
  auto-acoustic identification programs for northeastern bats', Journal of Fish and Wildlife

  Management 10(2), 346–361.
- Polasky, S., Carpenter, S. R., Folke, C. and Keeler, B. (2011), 'Decision-making under great
  uncertainty: environmental management in an era of global change', *Trends in Ecology*and Evolution **26**(8), 398–404.
- Reichert, B., Bayless, M., Cheng, T., Coleman, J., Francis, C., Frick, W., Gotthold, B.,
  Irvine, K., Lausen, C., Li, H., Loeb, S., Reichard, J., Rodhouse, T., Segers, J., Siemers,
  J., Thogmartin, W. and Weller, T. (2021), 'NABat: a top-down, bottom-up solution to
  collaborative continental-scale monitoring', *Ambio* **50**, 901–913.
- Reichert, B., Lausen, C., Loeb, S., Weller, T., Allen, R., Britzke, E., Hohoff, T., Siemers, J.,

  Burkholder, B., Herzog, C. and Verant, M. (2018), A guide to processing bat acoustic data

  for the North American Bat Monitoring Program (NABat), Technical report, Open-File

  Report 2018–1068, U.S. Geological Survey, Reston, Virginia, USA.
- <sup>714</sup> URL: https://doi.org/10.3133/ofr20181068
- Rodhouse, T. J., Ormsbee, P. C., Irvine, K. M. and Vierlin, L. A. (2012), 'Assessing the status

- and trend of bat populations across broad geographic regions with dynamic distribution models', *Ecological Applications* **22**(4), 1098–1113.
- Rodhouse, T. J., Rodriguez, R. M., Banner, K. M., Ormsbee, P. C. and Irvine, K. M. (2019),
- <sup>719</sup> 'Evidence of region-wide bat population decline from long-term monitoring and Bayesian
- occupancy models with empirically informed priors', Ecology and Evolution 9(19), 11078–
- 721 11088.
- Rodriguez, R. M., Rodhouse, T. J., Barnett, J., Irvine, K., Banner, K. M., Lonneker, J.
- and Ormsbee, P. C. (2019), North American Bat Monitoring Program regional protocol
- for surveying with stationary deployments for echolocation recording devices: Narrative
- version 1.0, Pacific Northwestern US, Natural Resources Report NPS/UCBN/NRR —
- <sup>726</sup> 2019/1975, National Park Service, Fort Collins, CO.
- Rojas, V. G., Loeb, S. C. and O'Keefe, J. M. (2018), 'False-positive occupancy models
- produce less-biased occupancy estimates for a rare and elusive bat species', Journal of
- Mammalogy 100(1), 212-222.
- Royle, J. A. and Link, W. A. (2006), 'Generalized site occupancy models allowing for false
- positive and false negative errors', *Ecology* 87(4), 835–841.
- 732 Silvis, A., Perry, R. W. and Ford, W. (2016), Relationships of three species of White-nose
- syndrome-impacted bats to forest condition and management, General Technical Report
- SRS-214, US Forest Service Southern Research Station, Asheville, NC.
- Stan Development Team (2020), 'RStan: the R interface to Stan'. R package version 2.21.2.
- URL: http://mc-stan.org/

- Stratton, C., Irvine, K. M., Banner, K. M., Wright, W. J., Lausen, C. and Rae, J. (in
- press 2022), 'Coupling validation effort with in situ bioacoustic data improves estimating
- relative activity and occupancy for multiple species with cross-species misclassifications',
- Methods in Ecology and Evolution.
- Sugai, L. S. M., Silva, T. S. F., Ribeiro, José Wagner, J. and Llusia, D. (2018), 'Terrestrial
- passive acoustic monitoring: Review and perspectives', BioScience 69(1), 15–25.
- Udell, B., Straw, B., Cheng, T., Enns, K., Winfred, F., Gotthold, B., Irvine, K., Lausen, C.,
- Loeb, S., Reichard, J., Rodhouse, T., Smith, D., Stratton, C., Thogmartin, W., Wiens, A.
- and Reichert, B. (2022), 'Status and trends of North American bats summer occupancy
- analysis 2010-2019 data release: U.S. Geological Survey data release'.
- USFWS (2020), Range-wide Indiana bat summer survey guidelines, Technical report, U.S.
- Fish and Wildlife Service Region 3, St. Paul, MN.
- 749 USFWS and USGS (2019), Testing procedures, performance criteria and approval process
- for automated bat ID software programs associated with range-wide Indiana bat sum-
- mer survey guidelines, Technical report, U.S. Fish and Wildlife Service Midwest Region,
- Bloomington, MN.
- Wade, P. R. (2000), 'Bayesian methods in conservation biology', Conservation Biology
- 754 **14**, 1308–1316.
- Williams, P. J. and Hooten, M. B. (2016), 'Combining statistical inference and decisions in
- ecology', Ecological Applications 26(6), 1930–1942.

- Wright, W. J., Irvine, K., Almber, E. and Litt, A. (2019), 'Code release for bat
- data analyses in "Modelling misclassification in multi-species acoustic data when es-
- timating occupancy and relative activity": U.S. Geological Survey software release,
- 760 https://doi.org/10.5066/P9QK83LD.'.
- Wright, W. J., Irvine, K. M., Almberg, E. S. and Litt, A. R. (2020), 'Modelling misclassi-
- fication in multi-species acoustic data when estimating occupancy and relative activity',
- Methods in Ecology and Evolution 11(1), 71–81.
- Wright, W. J., Irvine, K. M., Rodhouse, T. and Litt, A. R. (2021), 'Spatial gaussian pro-
- cesses improve multi-species occupancy models when range boundaries are uncertain and
- nonoverlapping', Ecology and Evolution 11(13), 8516–8527.

## 767 Tables

| Scenario      | No. Nights | No. Sites | Species | $\phi_k$     | $\psi_k$ | $\lambda_k$ | $p_k$ |
|---------------|------------|-----------|---------|--------------|----------|-------------|-------|
| 1             | 8, 16      | 55        | Spp 1   | (0.90, 0.35) | 0.25     | .3          | 0.26  |
|               |            |           | Spp 2   | (0.10, 0.65) | 0.75     | 10          | 0.999 |
| 2             | 8, 16      | 55        | Spp 1   | (0.65, 0.10) | 0.25     | .3          | 0.26  |
|               |            |           | Spp 2   | (0.35, 0.90) | 0.75     | 10          | 0.999 |
| 3             | 8, 16      | 55        | Spp 1   | (0.65, 0.40) | 0.25     | .3          | 0.26  |
|               |            |           | Spp 2   | (0.35, 0.60) | 0.75     | 10          | 0.999 |
| $\overline{}$ | 8, 16      | 55        | Spp 1   | (0.90, 0.35) | 0.50     | .3          | 0.26  |
|               |            |           | Spp 2   | (0.10, 0.65) | 0.75     | 10          | 0.999 |
| 5             | 8, 16      | 55        | Spp 1   | (0.90, 0.35) | 0.25     | .7          | 0.50  |
|               |            |           | Spp 2   | (0.10, 0.65) | 0.75     | 10          | 0.999 |

Table 1: Parameter settings used to generate autoID datasets for 55 sites and 8 or 16 nightly surveys consistent with field knowledge and published work on M. sodalis (a rare species; denoted as "Spp 1") and M. lucifugus (a common species; denoted as "Spp 2"). Simulated data assumes the information about auto-classifier performance identifying species is correct and constant for all sites and revisits. Note  $\phi_k$  has the columns as the true species identity and the rows refer to the autoID label. For example, under Scenario 1, autoID labels to species 1 are correctly assigned 90% of the time and are contaminated by false positives or incorrectly labeled as species 1 35% of the time, on average.  $\psi_k$  is the probability species k occurs at a site,  $\lambda_k$  is the relative activity rate for species k during a nightly survey, and  $p_k$  is the probability at least one call file is recorded for species k during a nightly survey.

## Figure Captions

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Figure 1. Conceptual diagram representing our simulation study comparing four analytical 760 approaches for determining local presence of rare bat species. The black pathways denote 770 Bayesian model-based approaches that allow for both explanatory modeling and local deci-771 sions regarding species presence. The grey arrows represent the fact using the MLE-metric 772 at the site-level (MLESite) to assess local species presence does not allow for estimating 773 species-environment relationships more broadly (i.e., explanatory modeling). The stippled 774 outlined boxes convey both the Remove and "MLESite" approach rely on the MLE-metric 775 calculation at the visit- or site-level to adjust for species misclassifications. Dashed circles 776 represent nodes that we investigated in the simulation study with accompanying factors (in 777 call-out boxes) that we varied either through the data-generating process (relative activity, 778 occurrence probability, and auto-classifier accuracy rates), design criteria (number of visits), or in the decision-rule applied to assign species presence at a site (cut-off values).

Figure 2. Comparison of average (thick line) and individual (thin lines) 95% posterior intervals from fitting Bayesian model-based approaches (2SppCt, Remove, or Naive). Rare species estimated probability of presence ( $\psi$ , top row), probability of detection (p, middle row), and relative activity ( $\lambda$ , bottom row) based on 16 visits and 55 sites under three different data-generating scenarios (corresponding column labels [ $\psi = 0.25, \lambda = 0.3$ ], [ $\psi = 0.50, \lambda = 0.3$ ], or [ $\psi = 0.25, \lambda = 0.7$ ]). Horizontal black lines reflect the parameter values used for generating the datasets. Coverage of the data-generating parameter values indicated by the interval color (red = poor, purple = decent). There were a few iterations of the

simulation that resulted in MCMC samplers that did not converge (R-hat > 1.1) for the 2SppCt model and these iterations were excluded before average posterior intervals were computed. Additional convergence details and scenarios included in Appendix S2: Figure S1-S2.

Figure 3. Comparison of decision error rates for deciding rare species presence or absence 793 fitting the count detection model (labelled 2SppCt darker green boxes), Remove occupancy 794 model (labelled light green Remove boxes), or MLESite (mustard colored boxes). For Remove 795 and 2SppCt, the posterior mean of the  $Z_{i1}$ -state  $Prob(Z_{i1}=1|y)>0.75$  was used for species 796 absence, and  $Prob(Z_{i1} = 1|y) > 0.25$  for species presence at a site i. The threshold-values 797 were selected to balance the (in)correct decision rates (See Appendix S2). The MLESite 798 used a p-value threshold of 0.10 in the decision-rule. Each dot represents the conditional proportion of sites with a specific decision given the known true state of species present 800 (Z=1) or absent (Z=0) for each of 50 simulated datasets with 55 sites each. The columns 801 correspond to the true Z-state and each row is the species site-level decision. All scenario results provided in Appendix S2, Figures S3-S5.

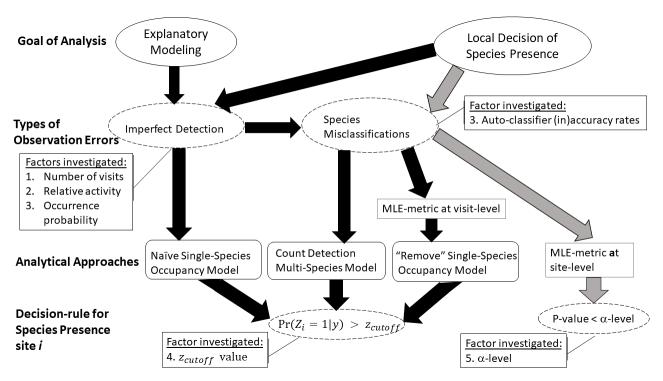


Figure 1: Conceptual diagram representing our simulation study comparing four analytical approaches for determining local presence of rare bat species. The black pathways denote Bayesian model-based approaches that allow for both explanatory modeling and local decisions regarding species presence. The grey arrows represent the fact using the MLE-metric at the site-level (*MLESite*) to assess local species presence does not allow for estimating species-environment relationships more broadly (i.e., explanatory modeling). The stippled outlined boxes convey both the *Remove* and "*MLESite*" approach rely on the MLE-metric calculation at the visit- or site-level to adjust for species misclassifications. Dashed circles represent nodes that we investigated in the simulation study with accompanying factors (in call-out boxes) that we varied either through the data-generating process (relative activity, occurrence probability, and auto-classifier accuracy rates), design criteria (number of visits), or in the decision-rule applied to assign species presence at a site (cut-off values).

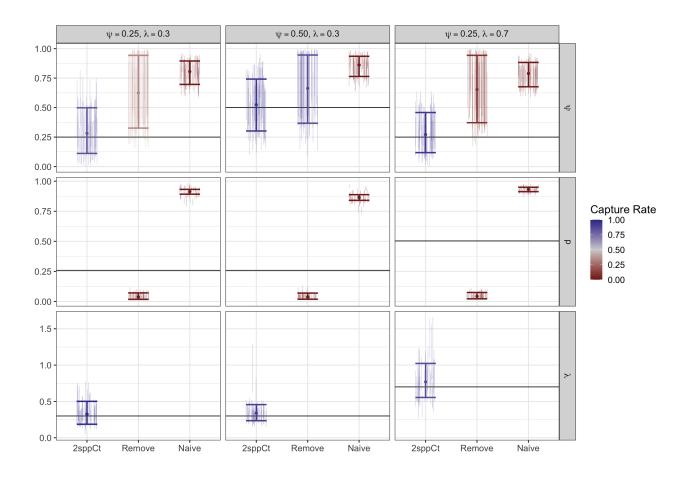


Figure 2: Comparison of average (thick line) and individual (thin lines) 95% posterior intervals from fitting Bayesian model-based approaches (2SppCt, Remove, or Naive). Rare species estimated probability of presence ( $\psi$ , top row), probability of detection (p, middle row), and relative activity ( $\lambda$ , bottom row) based on 16 visits and 55 sites under three different datagenerating scenarios (corresponding column labels [ $\psi = 0.25, \lambda = 0.3$ ], [ $\psi = 0.50, \lambda = 0.3$ ], or [ $\psi = 0.25, \lambda = 0.7$ ]). Horizontal black lines reflect the parameter values used for generating the datasets. Coverage of the data-generating parameter values indicated by the interval color (red = poor, purple = decent). There were a few iterations of the simulation that resulted in MCMC samplers that did not converge (R-hat > 1.1) for the 2SppCt model and these iterations were excluded before average posterior intervals were computed. Additional convergence details and scenarios included in Appendix S2: Figure S1-S2.

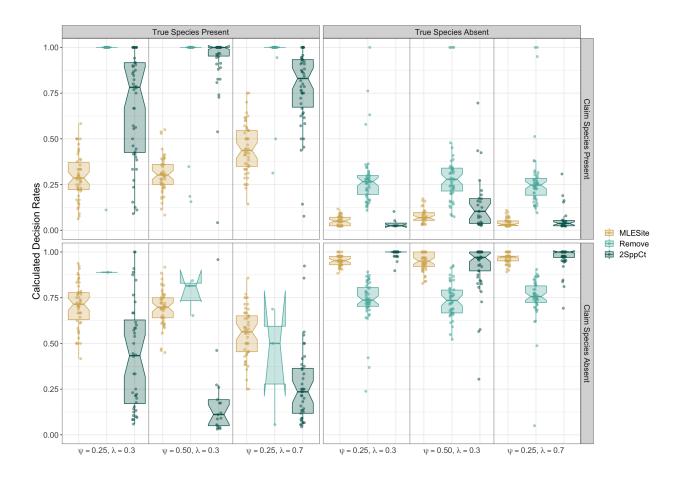


Figure 3: Comparison of decision error rates for deciding rare species presence or absence fitting the count detection model (labelled 2SppCt darker green boxes), Remove occupancy model (labelled light green Remove boxes), or MLESite (mustard colored boxes). For Remove and 2SppCt, the posterior mean of the  $Z_{i1}$ -state  $Prob(Z_{i1} = 1|y) > 0.75$  was used for species absence, and  $Prob(Z_{i1} = 1|y) > 0.25$  for species presence at a site i. The threshold-values were selected to balance the (in)correct decision rates (See Appendix S2). The MLESite used a p-value threshold of 0.10 in the decision-rule. Each dot represents the conditional proportion of sites with a specific decision given the known true state of species present (Z = 1) or absent (Z = 0) for each of 50 simulated datasets with 55 sites each. The columns correspond to the true Z-state and each row is the species site-level decision. All scenario results provided in Appendix S2, Figures S3-S5.

Appendix S1. Statistical assessment on determining local presence of rare bat species. K.M. Irvine, K.M. Banner, C. Stratton, W.M. Ford, and B. Reichert. *Ecosphere* 

## 808 Statistical Assumptions

An important consideration when fitting any statistical model is the underlying assumptions. If empirical data severely violate all or some of the assumptions, conclusions could be misleading. We made the following set of assumptions regarding bat acoustic data for our simulation study, and to show the connection between the MLE-metric p-value (Sec. 2.2; Britzke et al., 2002) and the recent multi-species count detection model developed for bioacoustic data (Sec. 2.3 Wright et al., 2020; Stratton et al., in press 2022).

The MLE-metric requires the following set of assumptions (A1 through A5) (Britzke et al., 2002).

- A1: The assemblage of bat species available for detection at a location or site is known.
- A2: An open-source machine learning algorithm or proprietary software is used to assign a species identity or label (hereafter, "autoID") to a high frequency recording (sequence of echolocation pulses). The (in)accuracy rates of the automatic classification process are known and uniform among the available species communities or sites.
- A3: A false positive is a result of a true positive from another species (a recording was

assigned the wrong species label).

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A5: The data available for analysis are the number or count of recordings per species (autoIDs) for each site and recording interval (e.g., a single night or aggregated over many nights). Under field conditions, the automated classification process could result in a large number of recordings without a single-species label (e.g., a frequency group or "noID"). We assume those observations would be discarded prior to analysis, thereby reducing the total number of recordings to just those identified to a single species.

A4: Identified recordings or observations are independent among species, nights, and sites.

## Mathematical connection between count detection posterior probability latent Z-state and "MLE" p-value

We show that the MLE-metric or the p-value from a likelihood ratio test for the null 833 hypothesis of species absence versus the alternative hypothesis of species presence in the 834 MLE calculation (Sec. 2.2) is related to the posterior probability species k is present at site 835  $i (Prob[Z_{ik} = 0|y] \text{ or } Prob[Z_{ik} = 1|y]) \text{ in the count detection model.}$  To simplify notation, 836 we consider 2 species (K=2) and assume both  $\psi$  and  $\lambda$  do not vary among sites i or nights 837 j (Eqn. 2 and 3 main text). However, the original Wright et al. (2020) multi-species count 838 detection model was developed for more than two species and was applied to an acoustic 839 dataset from Montana with seven species and an other category for the remaining species. 840 Another recent application applied the same model to a bat acoustic dataset from British Columbia, Canada composed of 17 species (Stratton et al., in press 2022). For a direct comparison to the MLE-metric calculation by Britzke et al. (2002) we assume the data available are the autoID counts per species  $(n_k)$  and the classifier (in)accuracy rates  $(\phi)$  are known. For clarity, we let  $\phi_{kk'}$  denote the probability that a call belonging to species k' is classified as species k, as in Britzke et al. (2002).

Under the count detection model, the sum of autoIDs for both species 1  $(n_{i1})$  and species 2  $(n_{i2})$  are conditional on the latent Z-states  $(Z_{i1}, Z_{i2})$ ;

$$[n_1|(Z_{i1}, Z_{i2}, \lambda_1, \lambda_2)] = Poisson[Z_{i1}\lambda_1\phi_{11} + Z_{i2}\lambda_2\phi_{12}]$$
(4)

849 and

$$[n_2|(Z_{i1}, Z_{i2}, \lambda_1, \lambda_2)] = Poisson[Z_{i2}\lambda_2\phi_{22} + Z_{i1}\lambda_1\phi_{21}].$$
(5)

Because the autoID counts are considered independent Poisson distributions, we can write the joint distribution for the autoIDs  $(n_{i1}, n_{i2})$  as the product of a multinomial and Poisson distribution from statistical probability theory.

The multinomial is as follows conditional on the total number of recordings detected and identified at a site i ( $N_i = n_{i1} + n_{i2}$ ) and the latent Z-states for a site i

$$[(n_{i1}, n_{i2})|(N_i, Z_{i1}, Z_{i2})] = Multinomial[N_i, \boldsymbol{\pi_i}], \tag{6}$$

855 where

$$\pi_{i1} = \frac{Z_{i1}\lambda_1\phi_{11} + Z_{i2}\lambda_2\phi_{12}}{Z_{i1}\lambda_1\phi_{11} + Z_{i2}\lambda_2\phi_{12} + Z_{i1}\lambda_1\phi_{21} + Z_{i2}\lambda_2\phi_{22}}$$
(7)

856 and

$$\pi_{i2} = \frac{Z_{i1}\lambda_1\phi_{21} + Z_{i2}\lambda_2\phi_{22}}{Z_{i1}\lambda_1\phi_{11} + Z_{i2}\lambda_2\phi_{12} + Z_{i1}\lambda_1\phi_{21} + Z_{i2}\lambda_2\phi_{22}}.$$
(8)

Both multinomial probabilities in Equation 7 and 8 simplify because  $\phi_{11}+\phi_{21}=1$  and  $\phi_{12}+\phi_{22}=1$  to the following,

$$\pi_{i1} = \left[ \frac{Z_{i1}\lambda_1}{Z_{i1}\lambda_1 + Z_{i2}\lambda_2} \right] \phi_{11} + \left[ \frac{Z_{i2}\lambda_2}{Z_{i1}\lambda_1 + Z_{i2}\lambda_2} \right] \phi_{12} \tag{9}$$

859 and

$$\pi_{i2} = \left[ \frac{Z_{i2}\lambda_2}{Z_{i1}\lambda_1 + Z_{i2}\lambda_2} \right] \phi_{22} + \left[ \frac{Z_{i1}\lambda_1}{Z_{i1}\lambda_1 + Z_{i2}\lambda_2} \right] \phi_{21}. \tag{10}$$

The distribution for the total number of recordings  $N_i$  conditional on the latent Z-states follows a Poisson (by the reproductive properties of independent Poisson distributions), as follows

$$[N_{i}|(Z_{i1}, Z_{i2})] = Poisson(Z_{i1}\lambda_{1}\phi_{11} + Z_{i2}\lambda_{2}\phi_{12} + Z_{i2}\lambda_{2}\phi_{22} + Z_{i1}\lambda_{1}\phi_{21})$$

$$= Poisson(Z_{i1}\lambda_{1} + Z_{i2}\lambda_{2})$$
(11)

863 and then

$$[Z_{ik}] = Bernoulli(\psi_k) \tag{12}$$

because of the independence assumptions for the latent Z-states.

The full likelihood is then the product over i and the Multinomial (Equation 6), Poisson (Equation 11), and then the Bernoulli (Equation 12), as follows

$$\prod_{i} [(n_{i1}, n_{i2}) | (N_i, Z_{i1}, Z_{i2})] [N_i | (Z_{i1}, Z_{i2})] [Z_{i1}] [Z_{i2}].$$
(13)

We draw the connection to the MLE calculation by equating both the statistical assump-

tions (previous section) and the bottom-level of the Bayesian hierarchical model (Equation 6 with simplified probabilities Equation 9 and 10) to the likelihood specified for the MLE calculation (Britzke et al., 2002).

In the two species case, Britzke et al. (2002) assumed a multinomial distribution for the autoIDs as follows (suppressing the additional sub-scripts of i and j for clarity),

Multinomial 
$$[N, (\phi_{11}\theta_1^B + \phi_{12}\theta_2^B, \phi_{21}\theta_1^B + \phi_{22}\theta_2^B)]$$
. (14)

The crux of our argument is that the same quantities  $(n_1, n_2)$  under the count detection model were modeled as,

$$\text{Multinomial} \left[ N, \left( \phi_{11} \frac{Z_1 \lambda_1}{Z_1 \lambda_1 + Z_2 \lambda_2} + \phi_{12} \frac{Z_2 \lambda_2}{Z_1 \lambda_1 + Z_2 \lambda_2}, \phi_{21} \frac{Z_1 \lambda_1}{Z_1 \lambda_1 + Z_2 \lambda_2} + \phi_{22} \frac{Z_2 \lambda_2}{Z_1 \lambda_1 + Z_2 \lambda_2} \right) \right]. \tag{15}$$

Then by matching up the parameters in Equation 14 and 15, we have  $\theta_k^B = \frac{Z_k \lambda_k}{\sum_k Z_k \lambda_k}$ .

The relative frequency for a species within the community  $(\theta^B)$  was decomposed within the hierarchical count detection model into the latent state of interest  $(Z_k)$  and the relative activity for a species  $(\lambda_k)$ . Therefore, a test for  $\theta_k^B = 0$  in Eqn 14 was similar to  $Pr(Z_k = 0|y)$  in Eqn 15 because if  $Z_k = 0$ , then  $\frac{Z_k \lambda_k}{\sum_k Z_k \lambda_k} = 0$ . An important distinction is that with the multi-species count detection model we account for potential false negatives at a site-level [non-detections] and variable species relative activity among sites and revisits.